

SPATIAL STRATIFICATION IN LITTER DEPTH BY FOREST-FLOOR SPIDERS

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ABSTRACT. Two novel sampling techniques were used to survey the spider community of the leaf litter in a deciduous forest in Kentucky, USA. Using modified pitfall traps and litter-grab techniques, we sampled separately the top, middle and bottom litter layers from April–October. Our sampling program captured over 3,000 spiders encompassing 18 different families. Both techniques revealed that the web-spinning families were more abundant in the lower litter layers. In contrast, the non-web building cursorial spiders, which actively pursue their prey, were more abundant in the top litter layer. Cursorial spiders, on average, were larger than the web-building spiders found in the leaf litter. Web-building spiders from the top litter layer were also larger than the web-building spiders caught in the middle and the bottom litter layers.

Comparison between the two sampling techniques revealed that the spider community profile is greatly influenced by the sampling method employed. The stratified litter-grab technique revealed the numerical dominance of Dictynidae (38% of the spiders captured) and Linyphiidae (32%), families that are predominately minute web-building spiders. In contrast, the pitfall-trap technique suggested Lycosidae (24%), a family of active foragers, to be numerically dominant, with Dictynidae representing only 1% of the spiders captured. The results indicate that major groups of spiders differ in their vertical distribution within deciduous leaf litter, and that sampling method can dramatically affect inferences about spider community structure.

Keywords: Micro-habitat segregation, leaf litter, pitfall trap, spider community

Spider communities that inhabit the leaf litter of an eastern deciduous forest floor frequently exhibit both high family diversity (>15 families) and numerical abundance (Kaston 1972; Dindal 1990; literature reviewed in Wise 1993). This pattern of high abundance and diversity is intriguing, considering that spiders are size-dependent generalist predators that often exhibit both intraguild predation and cannibalism (Polis 1988; Wise 1993; Wagner & Wise 1996, 1997). Research has suggested that the structural complexity of the leaf litter itself may facilitate the persistence of this high diversity of predators. In a series of field surveys and innovative field manipulation studies in mature deciduous forests in the eastern USA, Uetz (1975, 1977; 1979a, 1979b) and others (Bultman & Uetz 1982, 1984; Stevenson & Dindal 1982) ex-

amined the effects of litter complexity (e.g., leaf shape, litter depth), litter nutritional quality, prey abundance, and abiotic factors (e.g., moisture) on spider community diversity. Although prey abundance accounted for a statistically significant amount of variation in spider family diversity during the early summer months, litter depth, complexity and temperature were more important during mid- and late season (Uetz 1975, 1976, 1979a). One possible explanation may be that as the structural complexity of the litter increased, the surface area and diversity of potential foraging spaces within the leaves also increased. In particular, the spaces within curled leaves, the underside of twisted leaves, or the gaps between leaves create unique foraging sites for a diversity of spiders (Stevenson & Dindal 1982; Uetz 1991).

In addition to litter structural complexity contributing to spider family diversity, variety in spider foraging techniques may also allow for species coexistence. Spiders exhibit two basic forms of foraging techniques; entrapment, i.e. web-building spiders, or direct capture without the aid of a web, i.e. cursorial spiders (Wise 1993; Foelix 1996). These two forms of hunting techniques represent the ends of a continuum with numerous variations in between (Uetz 1992). Variation in foraging techniques may allow spiders to exploit different microhabitats within the leaf litter.

We propose that changes in structural and spatial complexity within the litter layer correlate with spider foraging methods to promote spider family diversity. In particular, spiders can exhibit habitat partitioning by restricting their foraging to particular litter layers. The layering within the litter often correlates with the age, and thus the degree of degradation, of different year-classes of litter: upper litter is composed of new, complete leaves with large air spaces between them, whereas the bottom litter layer consists of compacted humus. As a result we also expect spider species to segregate by size, with large animals in the upper, and smaller animals in the lower litter layers. The change in physical space within the different litter layers could also influence whether active pursuit or entrapment foraging method is favored. Based on these predictions we designed a field study to determine if forest-floor spiders exhibit spatial partitioning within the leaf litter in a deciduous forest. We devised two new types of sampling protocols, modified pitfall traps and stratified litter-grabs, to selectively sample the top, middle, and bottom litter layers in order to determine if spiders were non-randomly distributed within the litter according to their size and foraging mode.

METHODS

The research was conducted in an oak-hickory-maple forest in Madison County, Kentucky, USA. We devised two new sampling methods (stratified pitfall trapping and stratified litter-grab with extraction) to collect spiders at three different depths within the litter. The three litter layers corresponded to their age. The top layer was defined by the presence of curled, open-spaced leaves of the previous year. The thickness of the top litter layer fluctuates during the season. The middle layer (1–2 cm) sampled was formed by compressed leaves from several years in various degrees of decomposition, but still with a recognizable structure. The bottom stratum (1–2 cm) was identified as the amorphous humus layer that was delimited below by a sharp boundary of clay.

Stratified pitfall traps.—Each trap consisted of a 20 cm piece of ~ 7.5 cm diameter PVC pipe sleeve which housed a cup of 50:50 glycol:water solution with detergent added to reduce surface tension. A 1.2 cm slit was cut into the PVC sleeve either 5 cm from the end for the top or bottom-litter traps, or in the middle of the sleeve for the middle-layer trap. Two thin strips of metal flashing were attached at the top and bottom of the slit opening and extended 2.5 cm out from the pipe (Fig. 1). These lip barriers were designed to capture selectively only those spiders that moved laterally at the specific litter depth, by reducing accidental capture of animals making vertical migrations along the pipe sleeve. In the first month of sampling (April 1995), 30 pitfall traps were placed 3–6 m apart in repeating sequential order (bottom, middle, and top litter-layer sampled; $n = 10$ for each type of trap) along a circular transect 50 m in diameter. We recognized that this sequential protocol could create spatial correlation in the data; therefore, the pitfall traps were rearranged in random order for the remainder of the season (May–September 1995). The traps were emptied every two weeks.

Although pitfall trapping is an effective technique for sampling some spiders (Uetz & Unzicker 1976), the rate of capture is influenced by both abundance and activity levels of the target organism (Southwood 1978). Thus, less active spiders, e.g., many of the web-building guild, or very active and nimble spiders with excellent sense of sight, e.g., salticids (Land 1985) can be under represented in pitfall trap samples. To address this bias, a stratified litter-grab technique was developed that captured spiders that colonized layers of nylon mesh net placed at the top, middle, or bottom litter layers.

Stratified litter-grab technique.—Within the area circumscribed by the pitfall traps, two perpendicular 50 m transects were created to determine the random sampling areas to place stratified nets. Stratified litter-grabs were col-

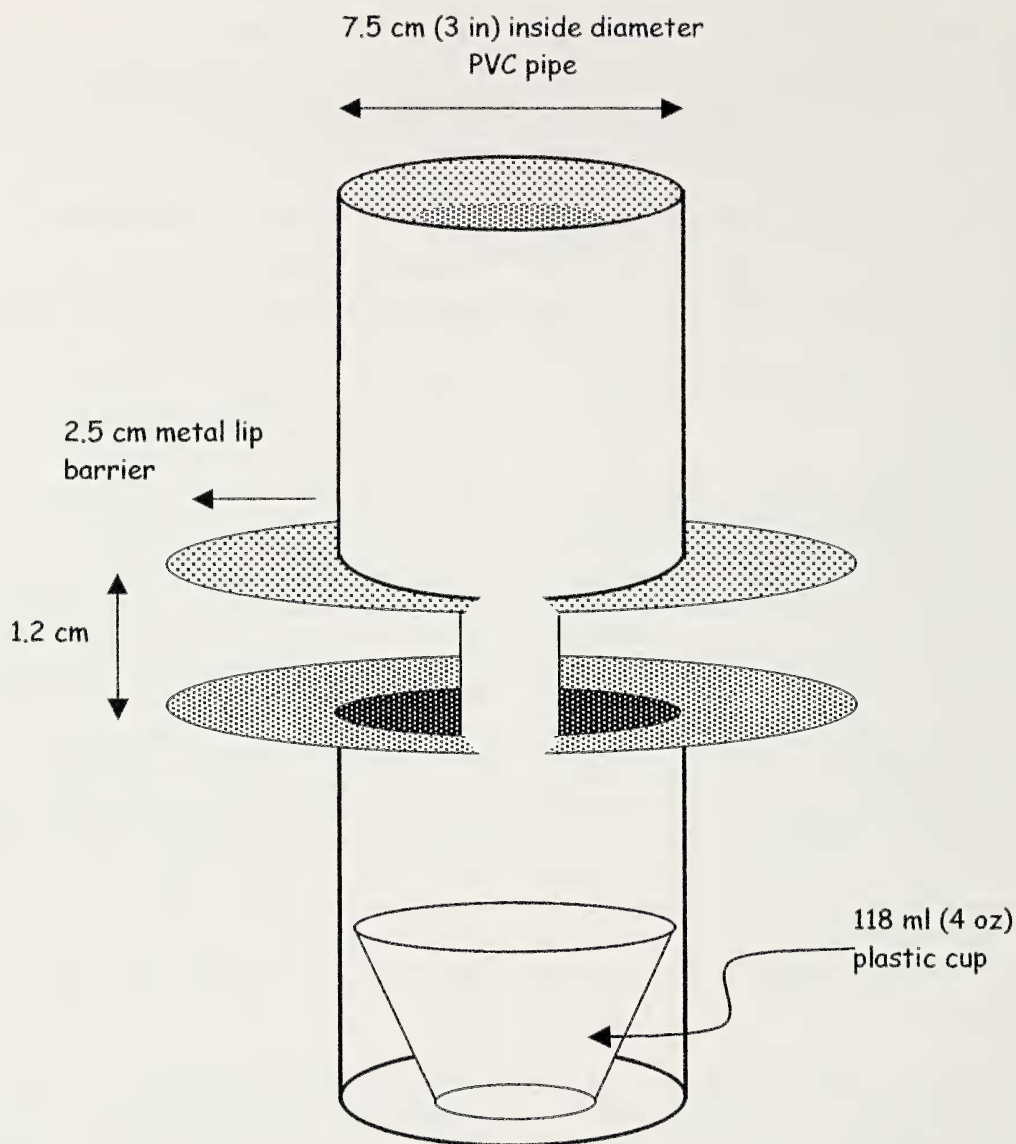


Figure 1.—Pitfall trap designed to selectively trap spiders moving laterally at a specific litter depth. The slit opening was set to one of three specific heights: the bottom, middle or top litter layer. The bottom layer sampled was the humus layer just above the soil. The middle layer was the compact litter layer between the humus layer and the top of the leaf litter. To sample the top layer, the lower lip barrier rested on top of the litter.

lected three times during the trapping period (May, July and October 1995) with each sample effort consisting of 10 litter-grab samples. Each litter-grab sample was created by first placing $0.5 \text{ m} \times 0.5 \text{ m}$ pieces of mesh (3 mm) netting between the top and middle, and between the middle and bottom, litter layers (Fig. 2). To install the nets, first a sharp knife was used to cut through the litter around the

area of the netting. Then the top and middle litter layers were carefully placed on separate pieces of netting. These two layers were then returned to their original position by stacking them, in order, on top of the undisturbed humus layer. The netting that separated the three layers was then secured in place by thin metal pins placed in each corner. After 4–5 weeks, a time period that allowed colonization by spi-

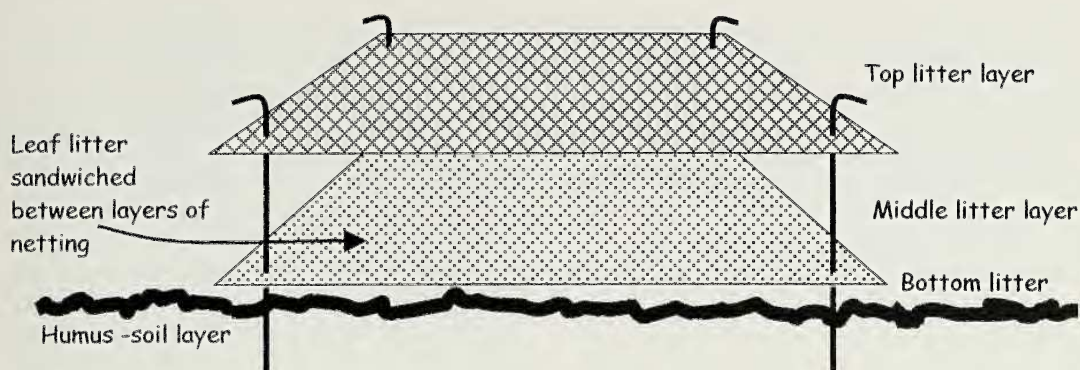


Figure 2.—The stratified litter grab technique employed two layers of netting that separated the top, middle and bottom litter layers.

ders, the anchor pins were gently removed from the four corners and the top and middle litter layers were quickly lifted and placed in separate plastic bags. The bottom humus layer was then collected by hand and placed in a third bag. All layers were first sorted by hand to remove the large spiders and were then extracted with a Tullgren funnel (Southwood 1978) to remove the smaller animals. Spiders were preserved in 70% EtOH, measured for total length (mm), and identified to family. Because we sought to uncover broad patterns, spider community structure was defined in terms of relative abundance of the major spider families. All spider families were assigned a foraging mode, either cursorial or web-building, based on published descriptions (Comstock 1940; Kaston 1972, 1981).

Statistical analysis.—Numbers of spiders in the samples often deviated substantially from a normal distribution; therefore, the non-parametric Kruskal-Wallis ANOVA (Siegel 1956) was used to determine if spider foraging modes were nonrandomly distributed across litter layers. If the Kruskal-Wallis test revealed a significant effect of litter depth, separate Mann-Whitney U tests (Siegel 1956) were conducted to test for differences between specific litter layers. Because we changed the trapping protocol for the pitfall traps after the first month of sampling, the pitfall data were analyzed as two different data sets: April, and the remainder of the months pooled for each trap. Each data set consisted of 10 independent estimates of numbers of spiders at each litter depth. In the analysis of the stratified litter-grab data, each sampling period (May,

July, October) provided an independent estimate of spider distribution, since new nets were installed each month. Thus, for the Kruskal-Wallis ANOVA of the litter-grab samples there were 30 (10 nets \times 3 sampling dates) independent estimates of numbers of spiders in each litter layer.

A cluster analysis (StatSoft 1995) was conducted to evaluate the similarity in composition of the spider communities, at the family level, for each depth within the leaf litter. Cluster analysis was also used to examine how similar the various spider families were in their distribution by litter depth, and how similar they were in frequency of capture by trapping technique. The cluster analysis was conducted on total counts of spiders in each family captured at each depth by each trapping method. The complete linkage (farthest neighbor) amalgamation method was employed to create the clusters. This method separates clusters based upon the greatest distance between any two objects in the different clusters (StatSoft 1995).

Spider size data was analyzed only from the stratified net samples. A Spearman Rank Order correlation was calculated between spider size, guild and litter depth (Sokal and Rohlf 1995).

RESULTS

Spider community.—The combined sampling effort yielded 3,204 spiders; 23% (747) were captured in pitfall traps and 77% (2457) were obtained from stratified litter-grab samples (Table 1). Five of the 18 spider families (Antrodiaetidae, Atypidae, Anyphaenidae,

Hahniidae, and Theridiidae) were represented by fewer than 10 individuals, and were excluded from the statistical analysis because of their rarity.

Spider foraging mode and litter depth.—Spiders numbers were not distributed uniformly across the litter layers; furthermore, the pattern of distribution with litter depth was different for the two spider foraging modes. In the April pitfall data, cursorial spiders were found significantly more often in the upper litter layers [$H_{(2,30)}$ (non-parametric Kruskal-Wallis ANOVA) = 16.5; $P < .001$], whereas web-building spiders were evenly distributed by litter depth ($H_{(2,30)} = 1.5$; $P = .48$) (Fig. 3A & B). The pitfall trap data for the remainder of the summer exhibited a similar pattern. Cursorial spider abundance varied significantly with litter depth ($H_{(2,30)} = 20.3$; $P < .0001$), with most of the cursorial spiders in the top litter layer (Fig. 3C). Although web-building spiders exhibited a trend towards having a greater abundance in the lower litter layer (Fig. 3D), the trend was not statistically significant ($H_{(2,30)} = 5.76$; $P = 0.056$). The stratified litter-grab technique revealed a clear relationship between spider abundance and litter depth. Similar to the pitfall trap data, cursorial spider abundance was significantly influenced by litter depth ($H_{(2,90)} = 53.58$; $P < .0001$), with more spiders in the top litter layer (Fig. 3E). Web-building spider abundance also exhibited a significant relationship with litter depth ($H_{(2,90)} = 39.93$; $P < .0001$), but the pattern was the opposite, with more web-building spiders found in the lower litter layers than the top layer (Fig. 3F).

Cursorial and web-building spiders displayed different distribution patterns, but within each foraging mode the two sampling methods revealed similar patterns of distribution across litter depth. However, the two sampling techniques yielded strikingly different estimates of the relative abundance of spider families within the same foraging mode (Table 1). Lycosid spiders were the most frequently captured cursorial spiders in the pitfall traps. In contrast, clubionids and gnaphosids were the most abundant cursorial spiders in the stratified litter-grab samples. For the web-building spiders, Agelenidae was the most abundant family captured in the pitfall traps, whereas Dictynidae was the most abundant

web-building family in the stratified net samples.

Spider community composition by litter depth.—Cluster analysis revealed that the composition of the spider community differed with litter depth and sampling protocol (Fig. 4). The spider community captured in the bottom and middle litter layers of the net samples differed distinctly from the spider communities represented in the top litter-layer samples from the net traps, and from the pitfall traps at all depths. The spider community from the bottom and the middle litter layers of the pitfall traps also differed distinctly from those represented in the top litter layers from both nets and pitfall traps.

Cluster analysis of spider families.—Cluster analysis of the spider families based upon trap type and litter depth revealed distinct groupings (Fig. 5). This analysis indicates which spider families are most similar based upon the depth of the litter they inhabit and the type of trap used to capture them. The first distinction was between two web-building families, Dictynidae and Linyphiidae, and all other spider families. The second major grouping segregated agelenids and lycosids from two other clusters that were composed of common cursorial spider families (Clubionidae, Gnaphosidae and Thomisidae) and an amalgamation of cursorial and web-building spiders (Amauroridae, Segestradae, Salticidae, Araneidae, Ctenidae and Nesticidae).

Spider size and litter depth.—Spider size differed with litter depth ($r_s = 0.259$; $P < 0.001$) and foraging mode ($r_s = -0.702$; $P < 0.001$) (Fig. 6). At all litter depths, cursorial spiders were significantly larger than web-spinning spiders. Among the web-spinning spiders, individuals from the top litter layer were larger than those caught in the middle and the bottom layers (Fig 6).

DISCUSSION

In a manner analogous to fish and plankton exhibiting species-specific vertical stratification in the water column (e.g., Holliday and Larsen 1979, Roepke 1993, Gray 1998), spiders exhibit taxon-specific (family level) vertical stratification within the depths of the forest-floor leaf litter. Our use of two separate and novel sampling methods, the stratified litter-grab and pitfall traps, indicated clear vertical stratification.

Table 1.—Mean and standard error for each Family captured at each litter depth (Bottom; Middle; Top layer) and trap type (Pitfall or Stratified Net). Mean represents average captured by trapping effort, e.g., number of spiders captured per pitfall trap per two-week sampling period or number of spiders captured per stratified net per month. Families identified with the "W" are web-building spiders; those labeled with a "C" are cursorial spiders. Families not identified by foraging guild were excluded from other analysis because of low capture rates. Numbers in bold represent the family with the highest average capture rate for that litter layer and trap type.

	Leaf litter depth					
	Bottom layer		Middle layer		Top layer	
	Pitfall	Nets	Pitfall	Nets	Pitfall	Nets
W	0.60 ± 0.10	2.0 ± 0.35	0.43 ± 0.07	2.24 ± 0.30	0.51 ± 0.10	0.53 ± 0.34
W	0	0	0.06 ± 0.03	0.14 ± 0.08	0.09 ± 0.04	1.40 ± 0.35
W	0.01 ± 0.01	0.81 ± 0.56	0	0.17 ± 0.17	0.03 ± 0.02	0
W	0.01 ± 0.01	16.11 ± 3.73	0.03 ± 0.02	16.28 ± 2.41	0.03 ± 0.02	1.07 ± 0.33
W	0.46 ± 0.10	11.81 ± 2.45	0.42 ± 0.09	13.83 ± 2.49	0.17 ± 0.06	2.87 ± 0.42
W	0.22 ± 0.05	0	0.07 ± 0.03	0	0.02 ± 0.02	0
W	0.01 ± 0.01	0	0.02 ± 0.02	0.10 ± 0.06	0.02 ± 0.02	1.20 ± 0.47
C	0.14 ± 0.05	0.26 ± 0.09	0.20 ± 0.05	1.83 ± 0.39	0.22 ± 0.04	5.13 ± 0.90
C	0.10 ± 0.04	0	0.06 ± 0.03	0.03 ± 0.03	0.09 ± 0.03	0.33 ± 0.19
C	0.09 ± 0.03	0.19 ± 0.08	0.29 ± 0.07	1.34 ± 0.32	0.64 ± 0.11	4.20 ± 0.96
C	0.17 ± 0.05	0.19 ± 0.08	0.56 ± 0.11	0.38 ± 0.13	1.28 ± 0.27	1.93 ± 0.67
C	0.03 ± 0.02	0	0.03 ± 0.02	0.24 ± 0.09	0.24 ± 0.06	1.0 ± 0.20
C	0.08 ± 0.03	0.11 ± 0.06	0.19 ± 0.05	1.55 ± 0.46	0.59 ± 0.13	4.53 ± 0.72
Antrodiaetidae	0.02 ± 0.02	0	0.01 ± 0.01	0	0.01 ± 0.01	0
Anyphaenidae	0.01 ± 0.01	0	0	0	0	0
Atypidae	0	0	0	0.03 ± 0.03	0.01 ± 0.01	0
Hahniidae	0	0	0.01 ± 0.01	0	0	0.07 ± 0.07
Theridiidae	0	0.11 ± 0.06	0	0.10 ± 0.06	0	0.13 ± 0.09

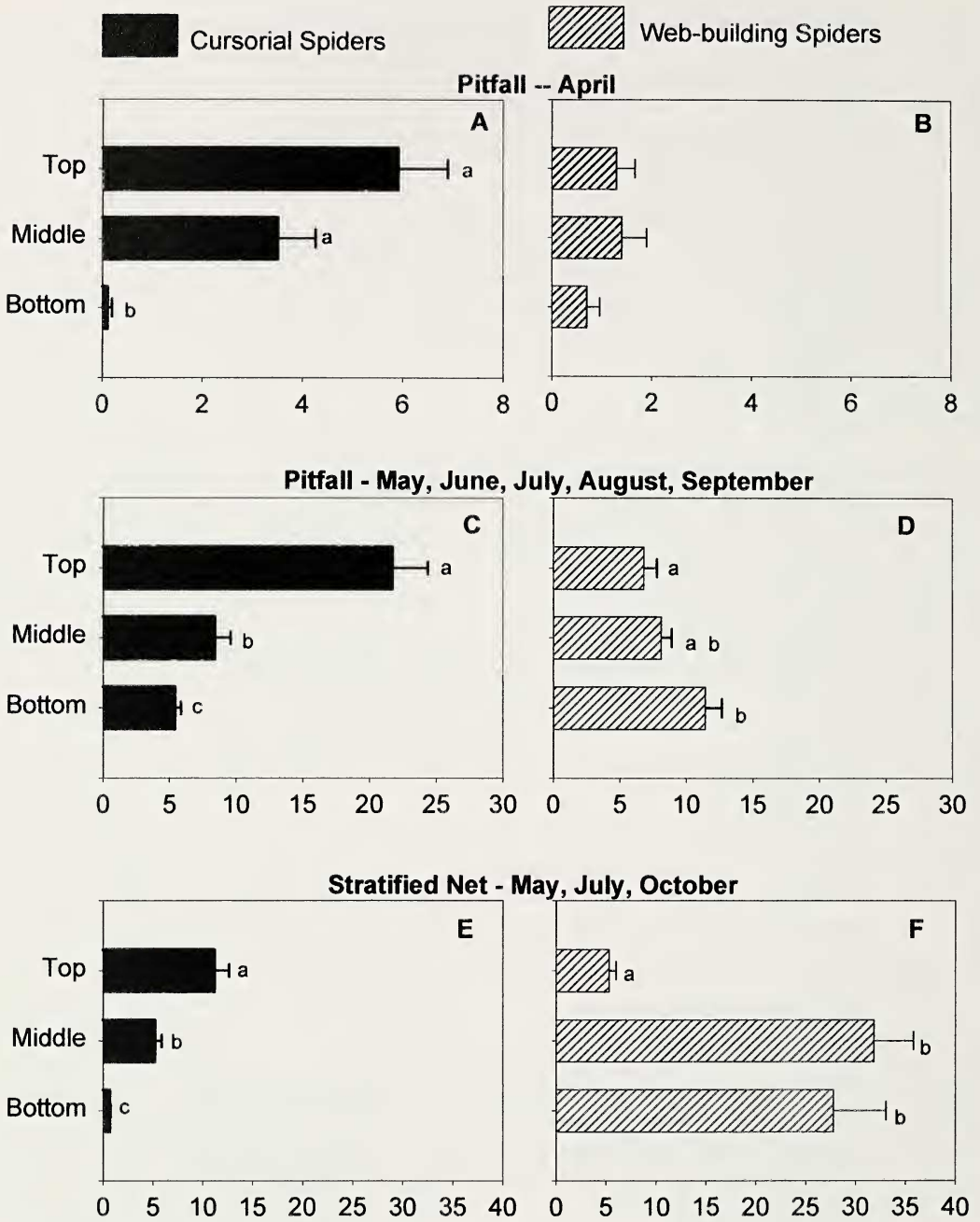


Figure 3.—Mean number (\pm SE) of spiders captured at each litter depth by both sampling methods (stratified litter grab [net] and stratified pitfall sampling). Plots A & B are from the pitfall data collected in April. Plots C & D represent data from the pitfall traps for the remainder of the season. Plots E & F represent data from the stratified litter grab technique. Bars labeled with the same letter are not significantly different based upon a Mann-Whitney U test. Absence of letters indicates that the Kruskal-Wallis H statistic was not significant at the 0.05 level.

Similarity of Spider Communities (Family level)

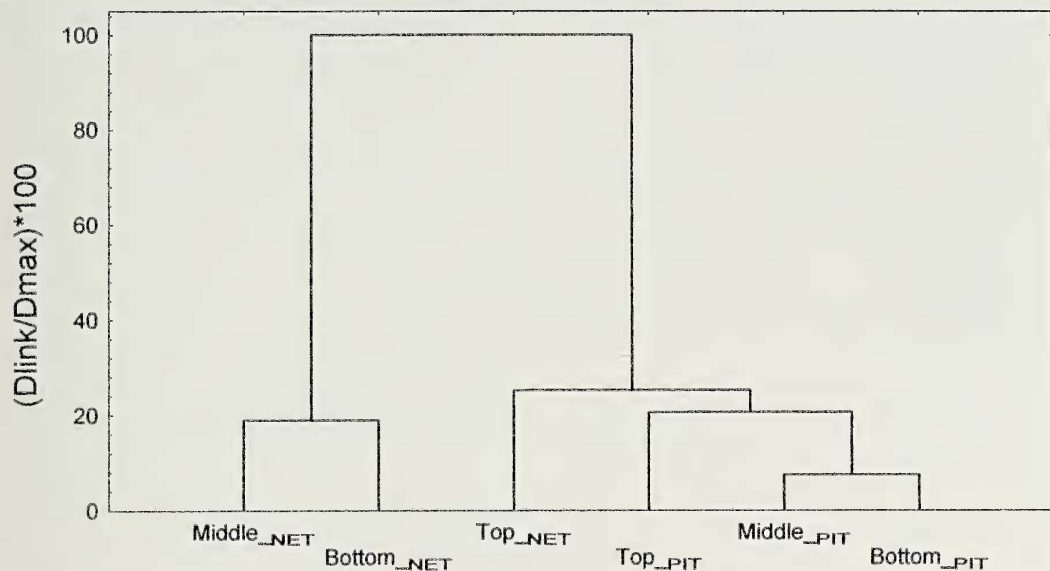
Complete Linkage
Euclidean distances

Figure 4.—Cluster analysis of spider community similarity based upon litter depth and trapping method. Spider family-level communities of the bottom and middle litter layers were distinctly different than the spider family-level communities found at the top litter layer. Spider communities were most similar between bottom and middle layers from the net data, and bottom and middle layers of the pitfall data. The composition of the spider community differed based upon sampling method.

Taxonomic groupings within the diverse spider community of the forest floor exhibit consistent microhabitat segregation correlated with litter depth. Cursorial spiders, which typically actively pursue or use a sit-and-wait strategy for prey capture (Uetz 1992), preferentially inhabited the top litter layers. In contrast, the web-building spiders were concentrated in the middle and lower litter layers. In conjunction with the shift in foraging mode with litter depth, body size of spiders decreased with litter depth. The main distinction in size was between those spiders captured in the top litter layer compared with those captured in the middle and bottom litter layers. The observed correlation in size of spiders with litter depth reflected large cursorial species occupying the upper spacious litter, while small web-building spiders occupied the older, compacted litter in the lower layers. On average, cursorial spiders were larger than web-spinning spiders, even when controlling for effects of litter depth. The low abundance of cursorial spiders in the bottom layer may be

related to their inability to penetrate the compacted, lower litter layers. However, space limitation does not explain the absence of the smaller web-building spiders from the top litter layers.

Various factors may be contributing to the difference in the size and type of spiders found with litter depth. Abiotic factors, such as moisture, light, and temperature, may influence spider distribution if they differ dramatically between the top and bottom of the litter layer. In the thick litter layer of a deciduous forest, relative humidity is higher in the lower layers compared to the surrounding air (Clary & Folliot 1969; Edwards & Sollins 1973; Swift et al. 1979). Unlike some insects, spiders lack the ability to extract moisture from water vapor in the atmosphere (Pultz 1987) and many are very sensitive to desiccation. Some spiders have evolved the tarsal organ, a specialized receptor on the leg used to detect changes in humidity (Foelix 1996). Web-building spiders such as Dictynidae, Amaurobiidae, and

Cluster Analysis of Spider Families

Complete Linkage
Euclidean distances

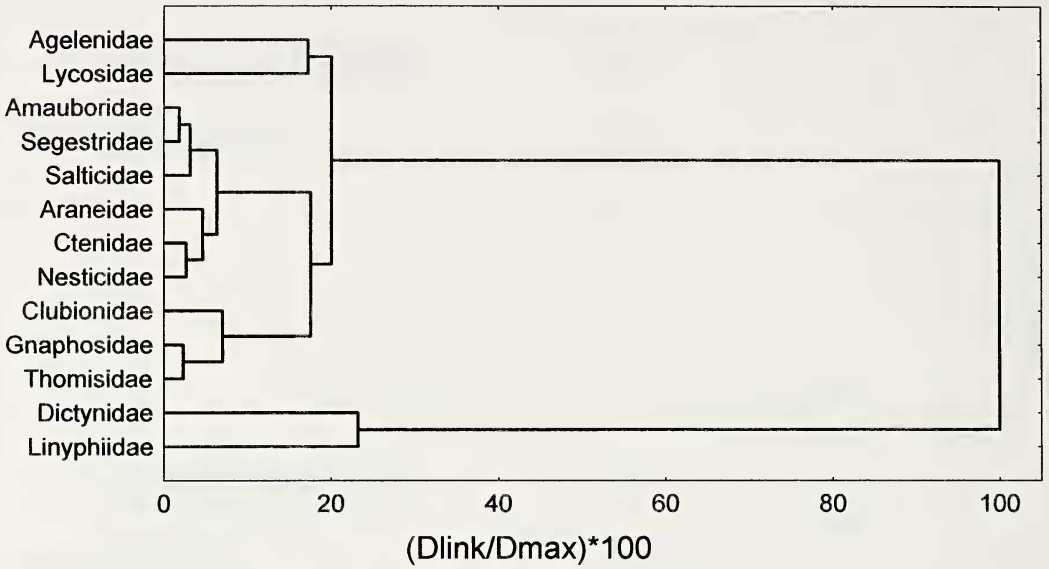


Figure 5.—Cluster analysis of spider families based upon litter depth and sampling method. Spider families closely grouped were similar in their use of litter depth and susceptibility to trapping methods.

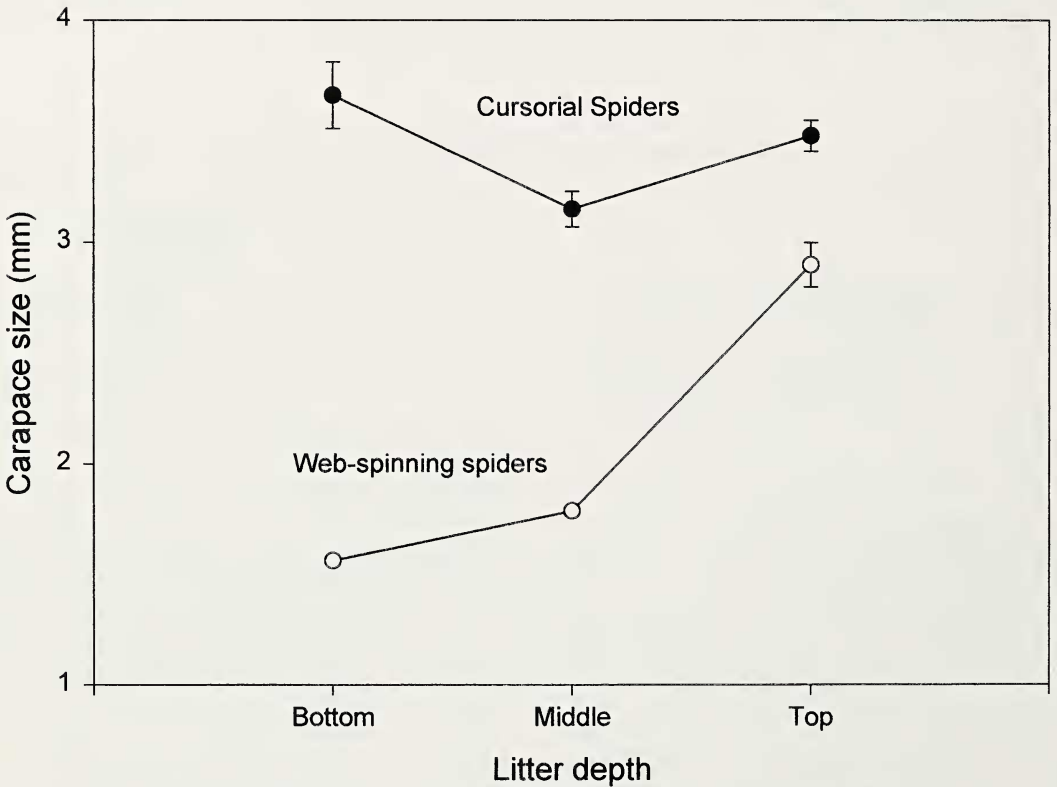


Figure 6.—Mean spider size (\pm SE) by foraging method and litter depth.

Linyphiidae may be restricted to the lower litter layers since these smaller spiders have a large ratio of surface area to volume, which could make hygrothermal regulation more difficult in the upper litter layers. In support of this interpretation, not all the web-building spiders were restricted to the lower layers. Based on the pitfall trap data, the large funnel-web agelenids were equally distributed across litter depths. The funnel-web design of some agelenid spiders allows them to live in a retreat that is deeper in the litter layer, thereby protecting them from desiccation (Riechert 1976). In contrast, the larger, more active cursorial spiders may be able to reside in the upper litter layer since they can more readily relocate to shady or moist locations when temperature and moisture levels are unacceptable (Humphreys 1987).

Ambient light intensity is another abiotic factor that may influence spider distribution within the leaf litter. Decreased light availability in the lower litter layers may hinder prey capture by visually oriented cursorial spiders. Although some cursorial spiders rely on vibratory cues to locate prey, reliance on visual cues for prey detection is important for lycosids and salticids (Land 1985; discussed in Foelix 1996). The lycosid *Schizocosa ocreata*, a species of the dominant wolf spider genus collected in this study, is known to rely on visual detection of prey when determining a foraging site (Persons & Uetz 1996), which may limit them to the upper litter layers. The importance of vision in prey capture in other cursorial spiders, e.g., Clubionidae and Gnaphosidae, is poorly understood. Web-building spiders typically have poorly developed eyes (Foelix 1996) and may be less hindered in capturing prey in the darker, lower litter layers.

Our sampling program captured over 3,000 spiders encompassing 18 different spider families. Comparison between sampling efforts, pitfall traps versus litter-grab sampling, indicates that the inferred spider community profile is greatly influenced by the sampling method employed. Studies that rely on pitfall sampling to characterize the leaf-litter spider community inherently over-emphasize the abundance of cursorial spiders in comparison to web-building species. In our pitfall traps, cursorial spiders made up 60% of the total spi-

ders captured; in comparison, in the stratified litter-grab samples cursorial species accounted for only 21% of the spiders collected. The largest discrepancy was in the representation of the web-building Dictynidae and cursorial Lycosidae. Data based on pitfall traps suggest that lycosid spiders are abundant and dictynid spiders are rare. However, density estimates from the litter-grab samples indicate the opposite. Average summer density for dictynids was about 124 individuals/m² in contrast to the average estimated density of lycosid spiders of 7 individuals/m². These results clearly show how spider activity and sampling method can bias the representation of a spider community.

Our data also indicate that the composition of the spider community at the family level changes from the top to lower litter layers. In the top layers the spider families representing cursorial species were the ones numerically dominant in the samples. In the middle and lower litter layers, those spider families recognized as web-building foragers were the numerically dominant group. We suggest that the complex 3-dimensional space within the leaf-litter layer may facilitate the high spider family diversity observed in the forest floor. Other researchers have found that the physical structure of the habitat itself directly influences spider community composition (Robinson 1981; Uetz 1991; Balfour & Rypstra 1998; Halaj et al. 1998). What is not clear is the relative role played by abiotic factors versus interspecies interactions in influencing the shift in spider community composition with litter depth. Future removal studies of some of the numerically dominant cursorial and web-building spiders within this system could reveal the role of biotic interactions in creating the observed community diversity and microhabitat distribution.

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